

## Use of sound and aerial chases in sexual recognition in Neotropical *Hamadryas* butterflies (Nymphalidae)

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**Abstract.** Neotropical *Hamadryas* butterflies are notorious for the clicking noise they produce in flight. Tests of the sound production capacity of nine species of *Hamadryas* and observations on aerial interactions of six species showed that, among the three species groups, only males of the *feronia* group produced sounds, whereas females of all species and males of the *februa* and *laodamia* groups never did so. Most of the aerial interactions occurred during mid-day, generally initiated by males in exploratory flights. Chasers were always males. Males engaging in chases with other males continually produced clicking sounds during the interactions whereas males chasing females usually restricted their auditory displays to the initial phase of the pursuit. In a cage containing 24 individuals of both sexes of six species of *Hamadryas*, males were involved in 100% of the aerial interactions observed, with one single male participating in 57% of them. The most chased individuals were females and males of *H. feronia*. There was no relation between the number of times an individual successfully defended a feeding perch and the number of aerial chases initiated. Sound production is probably involved in finding mates, while aerial chases may be used in the establishment of a dominance hierarchy among male *Hamadryas*.

**Key words:** agonistic interactions, behavior, butterflies, communication, *Hamadryas*, acoustic communication, sexual recognition, sound.

### INTRODUCTION

Butterflies communicate by means of a variety of stereotyped acoustic, visual, chemical, and tactile signals (Swihart, 1967; Wickman & Wiklund, 1983; Boppré, 1984; Silberglied, 1984; Bernard & Remington, 1991; Lees, 1992). Among these, acoustic signaling is relatively infrequently cited in the literature (Swihart, 1967). The Neotropical *Hamadryas* (Hübner, 1806) butterflies, a tight-knit group containing 20 species (Jenkins, 1983), are famous for their production of loud clicking sounds during aerial chases (Bates, 1865; Darwin, 1871; Swihart, 1967; Otero, 1990). Adult butterflies feed on tree sap and rotting fruits, and individuals of both sexes may display and fight to defend feeding sites from congeners (Marini-Filho, 1996). Ross (1963) classified *Hamadryas* as 'pugnacious,' although he did not observe site fidelity or other evidence for territorial behavior. *Hamadryas* butterflies are capable of hearing sounds produced by other conspecific butterflies and consider that once these sounds are produced during social interactions, these are probably involved in conspecific communication (Yack *et al.*, 2000). Yack *et*

*al.* 2000 also discuss that the possible origin of sound production in the Papilionoidea butterflies could be derived from bat-detection in the basal clade of Hedyloidea moths, thus being a degeneration of these former structures.

Although Seitz (1913) reported that almost all *Hamadryas* [members of the genus *Ageronia* and *Peridromia* (genus *Hamadryas* sensu Jenkins, 1983)] make sound on flight, species typical of dense tropical forests (e.g. *H. chloe*, *H. alicia*, *H. rosandra* and *H. velutina*; Jenkins, 1983) apparently do not make sounds. Otero (1986), based on the observation that males of *H. feronia* intensely produce sound when pursuing other *Hamadryas* in flight, whereas *H. februa* were 'mute' and performed a spiral flight, argues that the behaviors represent alternative means of sexual recognition in the genus. *Hamadryas* were placed by Jenkins (1983) in three species groups (subgenera) based mainly in wing venation differences (note that species names preceded by \* are possible exceptions): (1) *feronia* species group (subgenus *Hamadryas*), including *H. feronia*, *H. guatemalena*, *H. iphithime*, *H. epinome*, *H. fornax*, \**H. alicia*, \**H. rosandra*, *H. amphinome*, *H. belladonna*, *H. arinome*, (2) *februa* species group (subgenus *Ageronia*), including *H. februa*, *H. amphichloe*, *H. glauconome*, *H. honorina*, *H. atlantis*, *H. chloe*, *H. albicornis*; and (3) *laodamia* species group

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(subgenus *Peridromia*), including *H. laodamia*, *H. arete*, *H. velutina*.

The mechanism of sound production by *Hamadryas* is still subject of controversy. At least seven different places on the thorax, abdomen and fore wings have been proposed as sound-producing organs (Jenkins, 1983; DeVries, 1987; Monge-Nájera & Hernández, 1991; Swihart, 1967). Otero (1990) presents good evidence that *Hamadryas feronia* produce percussive sound through the striking of the wings. He points out that the structures responsible for the loud snapping sound are the swollen veins at the distal end of the fore wing discal cell. These modifications also occur in the Australian *Hecatesia* moths and were called castanets by Bailey (1978). Some Satyrinae species in the genus *Pharneuptychia* and *Euptychoides* also seem to have identical structures associated with sound production (Kane, 1982; Murillo-Hiller, 2006). According to Otero (1990), castanets were only observed in the males of the sound-producing *feronia* species, while males and females of *H. februa* in Venezuela do not show these structures. The swellings of the sub-costal venation of the forewings have also been supposed to be associated with sound production by Monge-Nájera and Hernández (1991), however, these authors pointed that swollen sub-costal veins occur in all *Hamadryas* species they dissected (*amphinome*, *feronia*, *guatemalena*, *glaunome*, and *februa*) independent of sex. Further studies made by Yack *et al.* (2000) contradicts the percussion mechanism arguing that sound can be produced by a single forewing, thus proposing a wing deformation mechanism for the production of sound. This 'flip-flop' changes the side of the wing concavity as shown in the photographs presented by Monge-Nájera *et al.* 1998.

In the present study we evaluate the sound production capacity of nine species of the genus *Hamadryas* and analyze the hypotheses related to the possible functions of sound production and aerial chases in sexual recognition. After determining which species and sexes are capable of producing sounds, we use behavioral and morphological data to conjecture if (1) aerial interactions with sound production are used for sexual recognition between *Hamadryas*, and (2) aerial interactions are related to the establishment of a dominance hierarchy between the males present in the feeding arena.

## STUDY SITES AND METHODS

Butterflies were captured using standard Van Someren-Rydon butterfly traps baited with a mixture of fermented sugarcane juice and banana (DeVries, 1987). Traps were set several times from 1992 to 2000

along the edges and interiors of forests and woodlands at eight different localities: Linhares Forest Reserve (tropical semi-deciduous forest), Linhares, ES, Brazil (19°04' S; 40°08' W); Santa Genebra Forest Reserve (subtropical semi-deciduous forest), Campinas, SP, Brazil (47°04' S, 22°50' W); Brasília Botanical Garden and Água Limpa Reserve (tropical cerrado savanna and gallery forest), Brasília, DF, Brazil (15°57' S; 47°56' W); Pipeline Road (tropical evergreen rain forest), Gamboa, Panama (09°10' N, 79°51' W); the restinga dry-forest of Praia das Neves (semi-deciduous tropical dune forest) ES, Brazil (21°18' S, 41°02' W); Ecological Station of the University of Minas Gerais (upland tropical semi-deciduous forest), Belo Horizonte, MG, Brazil (19°43' S, 43°57' W); Serra da Canastra National Park (cerrado savanna and gallery forest), MG, Brazil (20°14' S, 46°33' W); and the cerrado woodlands of Fazenda Jatobá, Correntina, BA, Brazil.

We tested freshly captured butterflies for sound production capacity by holding the hind wings closed over their backs with forceps and passing the fore wings below the hind wings, so that the fore wings were free to beat and produce their typical clicking sound (Otero, 1990).

Data on flight interactions were obtained from butterflies kept in an outdoor cage (4 x 6 m at the base and 4 m in height containing the trunks of two trees) set in a plantation of native trees in the Linhares Forest Reserve. This area was regularly used by at least five *Hamadryas* species. Caged butterflies permitted observations on butterfly social behavior during a period of *Hamadryas* scarcity between June 1993 and March 1994. Observations of flight interactions were all from October 1993 on 24 caged butterflies, comprising 13 males (m) and 5 females (f) *H. feronia*, 2 m and 1 f *H. amphinome*, 1 m *H. iphithime*, 1 f *H. arinome*, and 1 m *H. laodamia* (Table 1).

Butterflies were fed with fermented banana and sugarcane juice every morning. Each butterfly was individually numbered on the hind wing underside with India ink or marked with highly visible colored spots on the upper side of each fore wing to indicate its sex and species. For each interaction, the species and sex of both individuals and which of them was the chaser and the chased were recorded. Sounds produced and, when possible, the individual responsible for it were also recorded. Nomenclature is based on Jenkins (1983).

The non-parametric statistic Chi squared was used to test the heterogeneity of the interactions among the sexes while the binomial statistic (Z) was used to compare the distributions of probabilities of interactions among individuals of the same sex or species and those of different sex or species.



**Table 1.** Observed and expected [ ] number of aerial interactions from 24 caged *Hamadryas* butterflies kept in an outdoor cage ( $N = 129$  interactions). Expected values of the main diagonal were calculated as  $[n(n-1)/N] \times 129$ , while the other elements were calculated as  $(n^2/N) \times 129$ . FR = *H. feronia*, AM = *H. amphinome*, ARI = *H. arinome*, IP = *H. iphthime*, LA = *H. laodamia*.

	FR <i>m</i> (n=13)	FR <i>f</i> (n=5)	AM <i>m</i> (n=2)	AM <i>f</i> (n=1)	ARI <i>f</i> (n=1)	IP <i>m</i> (n=1)	LA <i>m</i> (n=1)
FR <i>m</i>	91 [55]***	28 [23]	1 [9]**	0 [5]*	2 [5]	6 [5]	0 [5]*
FR <i>f</i>		0 [7]***	0 [4]*	0 [2]	0 [2]	1 [2]	0 [2]
AM <i>m</i>			0 [1]	0 [1]	0 [1]	0 [1]	0 [1]
AM <i>f</i>					0 [0]	0 [0]	0 [0]
ARI <i>f</i>						0 [0]	0 [0]
IP <i>m</i>							0 [0]

Hypothesis tests for sample proportion vs. hypothesized value: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

Spearman rank correlation was used to assess the relationship between two discrete variables describing the number of events observed.

## RESULTS

**Sound production.** The sound production tests carried out with recently captured butterflies showed that only males of the five species of the *feronia* group (sub-genus *Hamadryas*: *H. feronia*, *H. iphthime*, *H. epinome*, *H. amphinome*, *H. arinome*) produced sounds under the test conditions (Table 2). These were also the only species in which one can perceive swollen veins in the middle of the proximal border of the males' forewings. The *feronia* group females and individuals of both sexes of the *laodamia* (*H. laodamia* and *H. arete*) and *februa* (*H. februa* and *H. chloe*) groups never produced sounds in the hand tests (Table 2) nor in the flight cage. Males of *H. feronia*, *H. epinome* and *H. iphthime* (*feronia*-group species) produced most sounds, whether in flight interactions, when perched over food, or while walking on tree trunks. Data assembled from the literature (Table 3) suggest that there may be variation in sound production capacity of some species; however, since many *Hamadryas* species have very similar color patterns, these results need confirmation.

**Flying chases.** Of the 104 observed flight interactions in which the departing points of the participating individuals were observed, 74 occurred between two *H. feronia* males and 23 between a male and a female *H. feronia*. The other 7 interactions involved a male *H. feronia* and another species. The most frequent interactions between two males were initiated by a flying chaser (64%), while the most frequent interactions between a male and a female were between perched individuals (39%) ( $\chi^2 = 58.7$ ,

$d. f. = 3$ ,  $P < 0.0001$ ). Aerial chases occurred almost exclusively during periods of intense sunshine, mainly from 1130 h to 1330 h on hot windless days. *Hamadryas* males commonly made exploratory flights ca. 1.5 to 2.5 m high, surrounding the two trees inside the cage. Such behavior normally stimulated other individuals in the cage to fly.

When encountering a perched individual, flying *Hamadryas* of the *feronia*-group frequently made a pendular flight display. This display comprised a semicircular flight with constant sound production for 5 to 10 s, 10 cm below the perched individual, which could be of either sex. Some perched individuals did not respond to the display, but others took flight after or ahead of the displaying individual. When this happened with two males, a chase was normally initiated with one or both butterflies vigorously producing sounds during the first 10-20 s of the interaction. During a chase both individuals flew rapidly and performed complex aerobatic maneuvers which included downward spiral flights, fast dives-and-rises, zigzags, and sudden, momentary (<1 sec) perches.

Twenty-five percent of the aerial chases ( $n = 27$ ) began when an individual walked on the trunk and found and touched another individual. Apparently individuals walking on trunks after feeding were deliberately looking for other *Hamadryas* with which to interact (and not for food). Another 33% of the aerial chases ( $n = 35$ ) began with a perched butterfly darting after a hovering individual, and 18% of the chases ( $n = 19$ ) began with a flying butterfly provoking a perched individual to fly using the pendular display. The other 24% of the aerial interactions ( $n = 26$ ) were initiated when two individuals met in flight; these occurred mainly during the hottest hours when many butterflies were flying. Interactions between more than two butterflies were not considered.

**Table 2.** Number of individuals producing sound in the hand tests carried out with males and females of nine *Hamadryas* species in Brazil and Panama.

Species group (Subgenus)	Species	Sex	Number producing sound	Number soundless	Percent individuals producing sound
<i>februa</i> ( <i>Ageronia</i> )	<i>februa</i> <sup>3, 6, 7, 8, 9</sup>	<i>m</i>	0	21	0
		<i>f</i>	0	18	0
	<i>chloe</i> <sup>8</sup>	<i>m</i>	0	3	0
		<i>f</i>	0	2	0
<i>laodamia</i> ( <i>Peridromia</i> )	<i>laodamia</i> <sup>2</sup>	<i>m</i>	0	8	0
		<i>f</i>	0	4	0
	<i>avete</i> <sup>2</sup>	<i>m</i>	0	1	0
		<i>f</i>	0	1	0
<i>feronia</i> ( <i>Hamadryas</i> )	<i>feronia</i> <sup>2, 4, 5, 6, 7, 8</sup>	<i>m</i>	35	7	83
		<i>f</i>	0	26	0
	<i>iphthime</i> <sup>2, 4</sup>	<i>m</i>	39	2	95
		<i>f</i>	0	20	0
	<i>epinome</i> <sup>2, 3, 8</sup>	<i>m</i>	17	1	94
		<i>f</i>	0	15	0
	<i>amphinome</i> <sup>2, 7, 8</sup>	<i>m</i>	18	3	86
		<i>f</i>	0	19	0
<i>arinome</i> <sup>2</sup>	<i>m</i>	5	0	100	
	<i>f</i>	0	5	0	

1) *Sensu* Jenkins (1983). Butterflies from: (2) Linhares, ES, Brazil; (3) Campinas, SP, Brazil; (4) Balboa, Panama; (5) Brasília, DF, Brazil; (6) Praia das Neves, ES, Brazil; (7) Belo Horizonte, MG, Brazil; (8) Serra da Canastra National Park, MG, Brazil; (9) Faz, Jatobá, Correntina, Bahia, Brazil.

**Table 3.** Summary of published reports of sound production in *Hamadryas* butterflies based on field observations (FO) and manual tests using Otero's (1990) hand test (OHT). References: (1) Jenkins (1983); (2) Ross (1963); (3) Monge-Nájera and Hernández (1991); (4) Otero (1990).

Group/Species	Sex	Locality	Method (FO/OHT*)	Sound production	Ref.
<i>februa</i> species Group					
<i>H. amphichloe</i>	?	Dominican Republic	FO	Yes	1
<i>H. chloe</i>	?	? (dense rainforest)	FO	No	1
<i>H. februa</i>	?	Mexico	FO	Yes	2
<i>H. februa</i>	???	???	FO	Yes	3
<i>H. februa</i>	<i>m</i> and <i>f</i>	Venezuela	FO/OHT	No	4
<i>H. guatemalena</i>	?	Mexico	FO	Yes	2
<i>feronia</i> species Group					
<i>H. feronia</i>	<i>m</i>	Venezuela	FO/OHT	Yes	4
<i>H. feronia</i>	<i>f</i>	Venezuela	FO/OHT	No	4

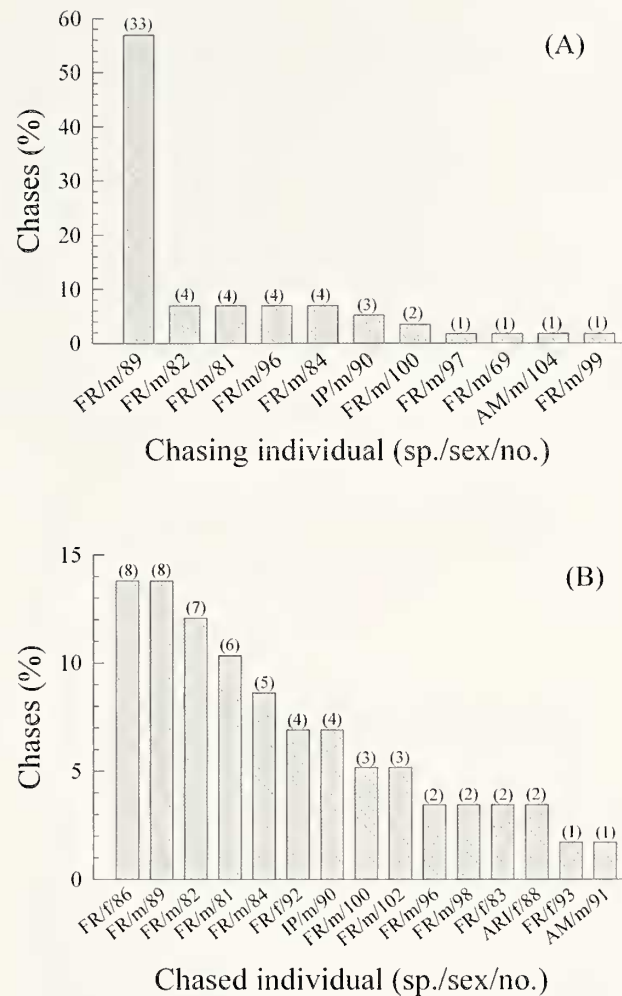
Of the 129 aerial chases with interacting individuals of known sex, among 17 m and 7 f, 76% ( $n = 98$ ) were between two males, which was more than expected ( $Z = 3.097$ ,  $P < 0.001$ ), 24% ( $n = 31$ ) with a male chasing a female ( $Z = -0.600$ ,  $P > 0.05$ ), and none with a female as the chaser, which was less than expected ( $Z = -3.802$ ,  $P < 0.001$ ) (Table 1). *Hamadryas feronia* participated in all interactions, generally chasing a conspecific (90.1%,  $n = 120$ ). Only 8 aerial interactions (6.2%) involved other species, and 7 of these were between *H. feronia* and a male *H. iphthime* (Table 1).

Chases between two male *H. feronia* occurred in a higher frequency than was expected ( $Z = 6.409$ ,  $P < 0.001$ ), and those involving a male and a female *H. feronia* occurred in a smaller frequency than was expected ( $Z = -2.721$ ,  $P < 0.005$ ) (Table 1). Chases involved fast flights and much sound production. These interactions usually ended with one of the individuals perching while the other continued flying. Interactions between a male and a female usually began with some sound production by the chasing male in a short period of fast flight, after which the male followed the female in a slow flight with little or no sound production until she perched. Frequently, the male would alight behind and court the female (described below). Individuals that were chased a lot seemed to avoid interactions and apparently flew less during the periods of greater exploratory flight activity.

The majority of the chases were carried out by only a few individuals (Fig. 1a), with one *H. feronia* (no. 89) performing no less than 57% of all chases (33 of the 58 chases by identified individuals). The next most active males initiated only four chases each. Three of the ten most chased individuals were females, but the frequency distribution of chased butterflies was much more uniform than the frequency distribution of the chasers (Fig. 1b).

Sometimes more than two *Hamadryas* engaged in aerial interactions. These interactions tended to be intense, long lasting, and difficult to keep track of the individuals. Most involved three or four individuals, but a few had up to seven. These happened when individuals met during exploratory flights in the hottest hours of the day and perched individuals joined the flying party. Some of these interactions in which all individuals could be identified consisted of two or more males chasing a female.

All *Hamadryas* species of both sexes may defend feeding sites through displays and physical interactions. However, there was no relation between the success of an individual in defending a feeding site and the number of times it chased after other individuals. Only one individual seemed to be efficient in both



**Figure 1.** Frequencies of aerial chases of identified *Hamadryas* individuals in a flight cage ( $n = 58$ ). **A)** Chases effected by a chasing individual. **B)** Chases suffered by a chased individual. Individuals are represented by a species/sex/number code: AM = *Hamadryas amphinome*, AR = *H. arinome*, FR = *H. feronia*, IP = *H. iphthime*, m = males, f = females, and the capture number of the individual.

tasks (*H. feronia* no. 89). Of the species engaging in aerial chases, *H. amphinome* did much better at defending feeding sites than at chasing other *Hamadryas* (Table 1; Fig. 2, Spearman correlation,  $N = 14$ ,  $R_s = 0.25$ ,  $t_{(n-2)} = 0.90$ ,  $P = 0.39$ ). Individuals of other species participated in less chases than was expected (Table 1).

**Courtship.** In the cage, six observations were made on male *H. feronia* courting females perched on a tree trunk. All of them around noon. Usually a male perched 5 to 10 cm behind a female and facing her and remained 1 to 5 min slowly opening and closing





study occurred around noon, simultaneously with the majority of the flight interactions. The sounds were produced at will during flight interactions by male butterflies. *Hamadryas feronia* has been proven to hear the sounds in the same acoustic range they produce (Yack *et al.*, 2000). Therefore, these situations may be used to promote sexual recognition which apparently takes place quickly at the very beginning of chases carried out by males after females. Thus, males initiating chases shift to courtship behavior almost immediately upon approaching a female or proceed in aerial pursuit when finding a male. Some moths (*Hecatesia thyridion*) and Satyrinae butterflies are among the few Lepidoptera known to produce high frequency sounds, similar to those produced by *Hamadryas* males, which are voluntarily used in intraspecific communication while in courtship flight (Bailey, 1978; Kane, 1982; Murillo-Hiller, 2006). Thus, it seems difficult to ascertain what role the clicking sounds play in *Hamadryas*' behavioral repertoire. We conjecture that the clicks are used as an early recognition of sexual partners and that sound intensity may also be used by females as a means to assess the male's fitness, as bigger healthier males may produce louder clicks. Behavioral experiments are needed to provide evidence for either hypotheses.

Although *Hamadryas* butterflies of both sexes defend feeding sites, the aerial chases observed here do not seem to be associated with resource defense or to territoriality (Ross, 1963). Food was provided *ad libitum* in two localized spots in the flight cage and the majority of the individuals had ceased feeding when aerial chases reached a climax (Marini-Filho, 1996). With the exception of one very successful male, males that had the greatest success in defending feeding sites were different from those that initiated aerial chases. While *H. feronia* was the species that performed the majority of the aerial chases, *H. amphinome* was the one that defended the feeding resource more fiercely. This is consistent with their size difference, as body size determines to a great extent the winner of those interactions (Marini-Filho, 1996).

Aerial chases apparently play two intimately related functions: the discovery of receptive females and the establishment of dominance hierarchies for mating priority, although we did not consider this during the experiment. Dominance hierarchies may be the result of natural selection over intraspecific differences in flight capacity or other fitness-related character, promoting the individual spacing in natural populations and enhancing the mating chances of hierarchically superior individuals (see Rutowski *et al.*, 1989), the priority order being generally established through previous agonistic encounters (Archer, 1988:

,114). The establishment of dominance hierarchies may come about by the recognition of the individual aggressiveness by the butterflies present in the same feeding area (usually one or a few tree trunks oozing fermenting sap). It is unlikely that monomorphic butterflies as other monomorphic insects are able to visually recognize others of the same or similar species (Ewing, 1984). Males and females of most species of the groups *feronia* and *februa* have a cryptic marbled color pattern, making them difficult to be recognized in flight. It is more likely that after a series of aerial chases the individuals present in the area can recognize behaviorally that there are other individuals more aggressive assuming then a submissive attitude, either evading chases or refusing to fly during the period of most aerial interactions. Possibly the most chased *Hamadryas* females were receptive, while non-receptive females would not stay close to the food source during the period of aerial chases, and would otherwise be looking for suitable host-plants for their larvae if they could have left the cage.

These results may also help the definition of the *Hamadryas* phylogeny once it seems that there is a high agreement between the ability to produce sounds observed on the males of the *feronia* species group and the inability to produce sound in the other two species groups (*laodamia* and *februa*). The ability of *H. amphichloe* to produce sound must be checked by hand test and further considered with the morphologic factors to find if it is an exception from this pattern or in fact more associated to the *feronia* species group than to the *februa* species group.

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